V. Geographic Differentiation in *Anolis oculatus* on Dominica

By James D. Lazell, Jr.

In 1956 Garth Underwood collected two series of *Anolis oculatus* in Roseau. Examining these and the specimens already in the Museum of Comparative Zoology he was led to suspect local population differences and therefore concluded in his report (1959) on the anoles of the eastern Caribbean that "clearly Dominica will require further careful examination."

In June of 1958 I was in Dominica specifically for the purpose of collecting some of the larger reptiles for the Philadelphia Zoological Gardens. At that time I collected a number of anoles at several different localities and noted striking differences in these series, apparently correlated with climate and elevation. This collection was donated to the Museum of Comparative Zoology and the following year I returned on behalf of that institution to determine what geographical differences existed and what the relationship of the apparent forms might be. In the course of eight weeks I collected over 500 specimens of this species from thirty localities; it now seems clear that in fact only one species is present but that it divides into four strikingly distinct geographic races.

Anolis oculatus is clearly a member of the *bimaculatus* group of Lesser Antillean anoles. (I follow Underwood [1959] in treating it as a distinct species.) It averages much smaller than *bimaculatus* (adult males: 70-76 mm snout to vent — except in the upland race, which approaches *bimaculatus* with lengths of up to 96 mm), and possesses weakly keeled ventrals and a double row of enlarged, sometimes swollen, middorsal scales. Generally the scales are convex, particularly on the head and neck. All forms show caudal cresting in the adult males and in some this is pronounced. Males also have an extensible nuchal crest.

Coloration and pattern vary widely within the species and furnish the principal basis for differentiation of the forms. The species as a whole shows a greater or lesser amount of spotting; from this feature the trivial name is derived. The spotting consists of alternating primary and secondary vertical rows of light spots — generally three to five of each along each side of the animal. The primary rows have their spots accentuated by dark, often black, pigment areas in the adult males; these dark pigment areas may be borders on several primary spots, or dots

or flecks surrounding or adjacent to a few primary spots, or large black patches forming a background for a number of primary spots and extending so as to nearly include the secondary rows. In one form the dark pigment areas may be occasionally completely lacking; in general this dark pigmentation is more pronounced on the larger male specimens and absent completely on the young and the half grown.

In ecology and habits *A. oculatus* seems plastic. It utilizes almost any available habitat from sea level to nearly 3000 feet. It appears, however, to be much more common in some areas than others. Along the Trans-Insular Road between Bells and Concord, for example, a distance of some ten miles, repeated trips resulted in the capture of only one specimen. In the same type of habitat and at similar elevations in other areas I had no trouble securing series. From just south of Roseau and just south of Point Mulatre an imaginary line can be drawn, south of which any anole is hard to come by, whatever the elevation or habitat one seeks them in. Why anoles should be so abundant in places like Roseau, the Fresh Water Lake, the Cabrits or Woodford Hill — each locality possessing a different form — and so scarce in certain other localities I leave to further investigation. Generally, however, the species is abundant enough so that several series of each form could be taken without difficulty and intermediate populations collected also.

This is a lizard with a preference for only vertical stations; it does forage on the ground and seldom ascends to a height of more than a few yards, but it seems to prefer sitting on a vertical substrate — whether it be a tree, bush, wall, road-cut, stone or building. It will occasionally seek shelter under stones, or between them, or in root masses if pursued. Further discussion will be found under the subspecies. (For distribution of subspecies see map, Plate 3.)

Anolis oculatus oculatus (Cope)

Xiphosurus oculatus Cope, 1879. Proc. Amer. Phil. Soc. **18**: 274.
Cotypes: USNM [1] Nos. 10139-48, 10150-1, 10153. Type locality, Dominica. Coll. Ferdinand Ober.

Cope's description does not mention a definite locality within the island, and the type series contains specimens that show occasional similarities to the northern Leeward coast form. Perhaps

[1] United States National Museum.

Ober's collection is composite, or represents an intermediate locality. However, most of the specimens described by Cope fit reasonably well with the southern coastal form, and some, like USNM 10145, closely resemble our figure of MCZ 60364 from Roseau. Thus it seems advisable to restrict the type locality to Roseau, the principal seaport of the island. The following is a description of fresh material collected by me.

Diagnosis. Ground color olive to tan; venter dirty yellow to whitish. Spots, both primary and secondary rows, less distinct than in ony other form and sometimes completely lacking. Black pigmentation adjoining spots very reduced or absent.

Coloration in life of adult males. (MCZ Nos. 60359-408, Roseau; coll. J. Lazell, 8 August, 1959.) Extremely variable; most specimens mottled olive or tan with dirty yellow venters and a yellowish tinge on the sides. Most specimens show at least a few spots in the primary rows; these are indistinct and show up best when there are black flecks or patches surrounding them; these patches occur in the majority of specimens around one to two, occasionally three, primary spots. In some specimens there is no black pigment present and in a few the primary spots have become so indistinct that the animal appears solid colored. The secondary spot-rows are generally faded to mere mottling between the primary rows. There is little if any marking on the head and neck and no distinctive coloration on the skin around the eye. (Top, Plate 1.)

Throat fan. Pumpkin yellow to orange.

Color of females and juveniles. Light olive to tan with whitish venters. Spots, if present at all, are very indistinct. There is usually a distinguishable dorsal stripe and often a lateral streak.

Additional series. MCZ Nos. 60425-40, Second Layou River Bridge, above Hillsborough; MCZ Nos. 60350-8, Hillsborough; MCZ Nos. 60409-14, Pointe Michel; MCZ Nos. 60415-24, Grand Bay. All of these specimens agree on all characters except that in the Grand Bay series there are no large adult males and no specimens showing any dark pigment areas.

Discussion. The southern leeward coast of Dominica is semi-xerophytic; this zone rounds the southern tip of the island and extends northward as far as the 1600 foot barrier of Morne Paix Bouche. This mountain, placed exactly on the coast, separates the drier area to the south from the wet lowlands or transitional forest of the windward coast to the north. Thus it is from just south of Morne Paix Bouche, around the southern tip and then

northward to the Layou Valley, that the nominate form of *Anolis oculatus* occurs. MCZ Nos. 60683-4, from Morne Paix Bouche, are almost typical *oculatus;* they differ somewhat in having more spotting than is usual and a richer, browner ground color. Thus I have considered them intergrades with the form of the more northern windward coast.

Caudal and nuchal crests are present in *A. o. oculatus,* but less evident than in any other form.

This is the smallest subspecies, the largest male measuring 73 mm snout to vent.

Anolis oculatus cabritensis subsp. nov.

Type. MCZ No. 60245, the Cabrits (= Prince Rupert Point), northwest of Portsmouth, Dominica. Coll. J. Lazell, 8 June, 1959.

Diagnosis. Ground color grey to pale tannish; venter bright yellow to pale peach color. Primary spots large, bold and well separated; secondary spots running into stripes. Black pigmentation enclosing several spots.

Coloration in life of adult male type and paratopotypes (males from series MCZ Nos. 60207-54). Very pale ash grey to tan; venters yellow to pale peach. Primary spots very large and bright; in most specimens they are blue — varying from sky blue to merely a faint blue-grey. These primary spots form two to three, occasionally four, extensive black pigment areas, corresponding to the primary spot rows. Each black patch contains from two to three primary spots and sometimes extending so far as to nearly surround the secondary spots. The secondary spots are less bright but quite bold and large and well run together, forming vertical stripes on most specimens, particularly posteriorly. The head and neck are stippled with whitish spots and streaks; the skin around the eye is the same color as this stippling. In nearly half the specimens the head has a very wine-red cast, particularly anterior to the eyes. In all cases the snout is at least browner than the ground color. (Bottom, Plate 1.)

Throat fan. Light bright yellow.

Color of females and juveniles (paratopotypes from series MCZ 60207-54). Pale grey ground color; venters yellowish. More spots and these more run together than in any other form. Dorsal and lateral striping also bolder.

Additional paratypes. MCZ Nos. 60299-317, Picard. This series, from a wetter area, is somewhat darker and more yellow than the Cabrits specimens; otherwise it agrees on all characters.

MCZ Nos. 60255-75, Pointe Ronde. These agree with the Cabrits series on all characters, but show slightly more yellow along the sides.

MCZ Nos. 60276-98, Grand Savanna. This series differs from the Cabrits specimens on no diagnostic characters, but shows a definite tendency for the bright yellow of the venter to invade the dorsal ground color — though it remains basically pale grey. There is much less evidence of red on the head anterior to the eyes, though this area is still generally browner than the rest of the ground color.

Discussion. The leeward coast of Dominica from the Grand Savanna to the Cabrits is the driest part of the island. Largely, it is truly xerophytic. This is the habitat of this palest, most boldly marked subspecies. In the wetter zones, like Picard, the population approaches the tan extreme of ground color. To the north *cabritensis* intergrades with the windward coast form (see below). Animals from the southern part of the range are brighter yellow and the yellow invades the dorsal ground color; in the northern part of the range there is a tendency toward red on the top of the head that is considerably less frequent in the southern population. In the male the heavy, bold spotting, large black pigment areas and stippling on the head and neck serve to distinguish this form immediately. Young and females are distinguished with equal ease by their pale grey ground color and large, bold markings.

This form shows the greatest degree of caudal cresting; the nuchal crest is also very well developed.

In size this seems to be the second largest — the biggest male measuring 75 mm snout to vent.

Anolis oculatus montanus subsp. nov.

Type. MCZ No. 60319, Fresh Water Lake, *ca.* 2500 feet. Coll. J. Lazell, 6 July, 1959.

Diagnosis. Ground color from light to dark green; venter paler green to rather bright metallic green. Spots small and bright; primary rows with spots larger and further apart, secondary rows with spots smaller and close together. Black pigmentation in one or more patches surrounding spots of primary row.

Coloration in life of adult male type and paratopotypes (males from series MCZ 60318-37 and 65919-48). Ground color from light leaf green to dark slatey green; venter paler green and dingier. Spots in irregular but recognizable rows — those of the

primary rows may have some (one to two — occasionally three) black patches surrounding one or two of the spots on each of the anterior rows. All spots rounded in shape and from white to lime green in color. Spotting extends profusely onto the head and neck — often well onto the ventral surface. Skin around eye sea green. (Top, Plate 2.)

Throat fan. Dark yellowish suffused with rusty brown. Scales light green.

Color of females and juveniles (paratopotypes from series MCZ 60318-37). Ground color green; venter often metallic looking. Spots small and fairly profuse. Fans dark brick-red. Dorsal stripe and lateral streak usually present.

Additional paratypes. MCZ No. 60338, Gleau Gomier, at the Old Carib Trace, *ca.* 2000 feet. MCZ Nos. 60339-49, Fond Hunt, *ca.* 2000 feet. These series agree in all characters with the topotypic series.

Discussion. This form is found throughout the central mountain range in rain forests over 2000 feet, approximately, and up to nearly 3000 feet. Evidence of its genetic influence can be found in the presence of greener coloration in surrounding populations at elevations above 800 feet. From this level spotting changes clinally upward until it becomes consistent as that characteristic of the montane subspecies at about 2000 feet. It is interesting to note that no evidence of *montanus* influence exists in the specimens taken on Morne Paix Bouche, *ca.* 1600 feet, on the coast, and thus the distance inland seems to be a factor as well as the elevation itself. The northern high point of the island, Morne au Diable, provides a series taken between 2000 and 2500 feet. These animals show definite *montanus* characters, but more closely resemble the windward coast form. This highland area is separated from the main ridge of mountains on the island by a gap that is little higher than 200 feet. Specimens taken at Dos D'Ane, at the high point of the gap, *ca.* 200 feet, show no evidence of *montanus* influence; the population on Morne au Diable is thus separated from the rest of the *montanus* range and surrounded by the windward coast form and its intergrades with *cabritensis.*

In this subspecies the tail crest is usually well developed but the nuchal crest is as little in evidence as in *A. o. oculatus.*

This is certainly the largest subspecies; a number of adult males measure between 76 and 85 mm. snout to vent and one, MCZ No. 60344, from Fond Hunt, is probably the largest *Anolis oculatus* ever collected — measuring 96 mm snout to vent.

Anolis oculatus winstoni subsp. nov.

Type. MCZ No. 60467, Woodford Hill. Coll. J. Lazell, 29 June, 1959.

Diagnosis. Ground color coffee; venter deep peach to bright yellow. Little distinction between primary and secondary spots; spots tend to be rounded in outline and small to moderate in size. Black pigmentation rudimentary, at most dark borders to the spots.

Coloration in life of adult male type and paratopotypes (males of series MCZ Nos. 60441-90). Ground color coffee, varies from light to dark. Venter usually deep peach, sometimes shading to bright yellow. The animals are heavily peppered with small to moderate sized white dots that often have some indication of dark bordering, though never the black patches found in the other forms. There is little if any distinction between primary and secondary spot rows in most specimens. Spots extend heavily onto the head and neck; skin around eye varies from white to sky blue. (Bottom, Plate 2.)

Throat fan. Deep pumpkin yellow.

Color of females and juveniles (paratopotypes from series MCZ 60441-90). Ground color coffee, sometimes with faint olive tint. Spots less obvious than in adult males and somewhat obscured by longitudinal streaking.

Additional paratypes. MCZ Nos. 60491-507, Penville; MCZ Nos. 60508-20, Blenheim; MCZ Nos. 60640-4, Hatten Garden; MCZ Nos. 60521-4, Salybia; MCZ Nos. 60525-38, Castle Bruce; MCZ Nos. 60539-50, Rosalie; MCZ Nos. 60622-39, La Plaine. All agree with the topotypic series in all characters.

Discussion. This form has the widest range of the four, being found in the transitional forests or wet lowlands all along the windward coast from the northern point, Penville, to the barrier of Morne Paix Bouche, south of which the country becomes drier. Specimens taken at Pointe Mulatre, just north of Morne Paix Bouche, fit *winstoni* well, but are paler and more olive with spotting less distinct; this then is the zone of intergradation with the nominate form. *A. o. winstoni* intergrades with *cabritensis* at Dos D'Ane, between the central massif and Morne au Diable, and on the northern coast as far south as the Cabrits peninsula. It intergrades with *montanus* on Morne au Diable and undoubtedly all along the eastern slope of the Morne Grand Bois-Diablotin massif. Ecologically, then, this is the form of the wet lowlands.

The nuchal crest is more pronounced in *winstoni* than in any other form, though the caudal crest is not usually so well developed as in *cabritensis*. There is a tendency in old males for the scales within the white dots to become swollen and tubercular; this occurs to slight extent in both *montanus* and *cabritensis* in occasional specimens; this never occurs in *oculatus*. In no case, however, is it as pronounced or common as in *winstoni*.

In size this form falls between *oculatus* and *cabritensis*, with the largest male measuring 74 mm snout to vent.

This subspecies is named for Charles A. Winston, Manager of Woodford Hill Estate, and his family. His knowledge of the island's wildlife and his constant willingness to assist me in my wanderings over the island made possible the collection here reported.

Discussion

There are several additional series of *Anolis oculatus* which are pertinent to the discussion of this animal. These include MCZ No. 28593, Roseau; coll. Thomas Barbour, 1929. This specimen is badly faded, but shows the black pigment areas well and these would definitely relegate it to the subspecies *oculatus*. MCZ Nos. 55706-8, Rouseau; coll. G. Underwood, 28 July, 1956 — also typical *oculatus*. MCZ No. 59162, near Fresh Water Lake, *ca.* 2000 feet; coll. Dr. Joseph Seronde, 3 July, 1959. This specimen is apparently a typical young *montanus*. Two other series present difficulty:

MCZ No. 6160 (24), Roseau; coll. S. Garman, 1879. This appears to be a series of specimens intermediate between *oculatus* and *cabritensis*, possibly from the coastal area around St. Joseph or Machouchery, eight or nine miles from Roseau. In fact, this series agrees quite well with my own from Machouchery (MCZ Nos. 60645-54) which are intermediate in characters. This area is close enough to Roseau so that it seems feasible that the series in question could have been collected there; in fact, since the large estates on the island were in this area, it seems quite probable that Garman headed in that direction. (Note that some of Cope's type series seem intermediate in the same way but to a lesser degree.)

The second series, MCZ No. 6159 (14), Portsmouth, coll. S. Garman, 1879, is more difficult to interpret. Three appear to be *winstoni* × *montanus* intergrades, possibly from the hills to the

northeast of Portsmouth; proceeding in this direction the influence of the coastal *cabritensis* is quickly lost. Eight are so badly faded that at first they suggest *oculatus* of the south coast; this I believe is entirely due to the fading though, for where any indication of spotting remains it would indicate some head markings, making a northern locality likely. The three remaining juveniles are badly discolored and cannot be assigned to any particular form. It seems at least plausible that all of these came from the hills above Portsmouth.

Garman states in his account of these animals (1887) that they were taken "at several points on Dominica," though only two localities appear on the labels. He includes a description of them that certainly fits the species, but which cannot be assigned to any one of the subspecies.

Possibly these old collections serve to emphasize the remarkable differences that can take place on an island like Dominica within a relatively small area — literally within a comfortable walk! The island is only twenty-eight miles long and approximately seventeen miles wide and it may at first look seem strange that subspecies differentiation could take place on it at all. However, when one considers that Dominica's central highlands rise to nearly 5000 feet in several places and that the prevailing wind direction is constantly from the northeast then the wide differences that exist in habitats and ecologies become clearly explicable.

The top and windward side of the island are blanketed with rain forest nearly down to sea level, where cultivation has not cleared the original vegetation. Along the windward coast is a broad transitional zone, which gives way on the leeward coast and southern tip to semixerophytic and xerophytic dry scrub woodlands and cactus country. The coast that lies in the lee of the huge massif of Morne Diablotin is virtually deprived of any rainfall — at least by comparison with the country to the windward of it.

The floral ecology of Dominica then divides into strikingly different zones that correspond remarkably with the distributions of the four geographic races of *Anolis oculatus* (Hodge, 1954).

In summation, it seems evident that the differing ecologic zones on a single island, such as Dominica, are more effective in differentiating forms of reptile life than are barriers, like water expanses, between islands of similar ecology. We need only compare Dominica with Antigua and Barbuda in the Leeward Islands to the north: even between these islands separated by

forty miles of sea there is little if any noticeable difference in the *Anolis* population. Both are low, dry islands with only pockets of wetter vegetation. Ecologically the two are virtually the same — a far cry from the situation that obtains in moving from one side of the island of Dominica to the other.

TABLE OF DIAGNOSTIC CHARACTERS
in
Anolis oculatus Subspecies

	oculatus	*cabritensis*	*montanus*	*winstoni*
Throat fan color	Pumpkin yellow	Light bright yellow	Dirty reddish	Pumpkin yellow
Dorsal spotting (white)	Indistinct primaries; Secondaries mere mottling	Large, bold primaries; Secondaries bold, run together	Small, round alternating primaries and secondaries	Small, bold; little differentiation
Black pigment areas	Variable; small — 0 to 3 present	Large; extensive, 2 to 4 present	Small; 1 to 3 present	Reduced to mere dark bordering
Ground color	Olive to tan	Pale grey to tan	Green	Coffee
Venter color	Dirty yellow to white	Yellow to pale peach	Green	Peach to bright yellow
Tail crest	Low	High	Moderate	Moderate
Size (maximum) (snout to vent)	73 mm	75 mm	74 mm	96 mm